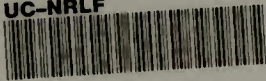


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ZOOLOGY

Vol. 1, No. 7, pp. 227-268, Pls. 20-23

June 1, 1904

THE STRUCTURE AND REGENERATION
OF THE POISON GLANDS
OF PLETHODON

BY

C. O. ESTERLY



BERKELEY

THE UNIVERSITY PRESS

PRICE \$0.50

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THE STRUCTURE AND REGENERATION
OF THE POISON GLANDS
OF PLETHODON.

BY
C. O. ESTERLY.



It has long since been held that the skin glands of both the Urodela and the Anura are of two kinds. This distinction was first made by Ascherson '40 in an investigation of the glands in the web of live frogs, and was based upon the size, shape, and location of the glands without regard to function or microscopic structure. That the skin of Amphibians secretes a substance other than the well-known mucus, and clearly poisonous, has been shown by many physiological and toxicological experiments and investigations (Albini '56; Boulenger '92; Calmels '83; Capparelli '83; Dutarte '89; Gratiolet and Cloez '51-'52; Hubbard '03; Phisalix-Picot '00), and the facts gained from experiment are upheld as far as possible by histological evidence. Microscopic examination shows that there is more than one kind of gland. (Aneel '02; Coghill '99; Eberth '69; Eckhard '49; Engelmann '72; Hensehe '56; Leydig '76 a; Paulieki '85; Phisalix-Picot '00; Schultz 89; Seeck '91; Stieda '65; Szezesny '67; Wiedersheim '86). These have generally been distinguished as granular (Körnerdrüsen) and clear, according to the appearance of the secretion contained in them, the former having been almost unanimously looked upon as making the poison series, the latter the mucous series. The suggestion has been made, however, that the various glands are only the young and old stages of one sort of gland (Junius '98), and this question will receive further consideration in the present paper.

The poison glands are in most cases much larger than those of the mucous variety, and their enormous cells (Riesenzellen of Leydig) completely fill the interior of the gland so that there is no lumen. This character distinguishes these glands from the others, which are provided with a low, cubical epithelium surrounding a capacious lumen. (Pl. XX, Fig. 2.) The mucous secretion filling the lumen is very distinct from the heavily granular contents of the cells of the poison glands. (Pl. XXIII, Fig. 31.) The two sorts of glands are further distinguished by other features, chief of which is the staining reaction of the mucous secretion (Nicoglu '93; Hoyer '90). These observers used thionin as a specific stain for mucus and found that the small glands stain rose-red while the others are uncolored.

The foregoing general facts have been determined chiefly upon the Anura and the various European Salamanders, especially Triton and Salamandra. But *Plethodon oregonensis*, a salamander found about Berkeley, forms a particularly interesting object for the study of the poison glands because of their unusual development on the tail of this animal. This seems to be a protective character associated to some extent with the ability of the animal to throw off its tail under stress of circumstances. It has been shown by experiment that the secretion of the glands of the tail is poisonous or obnoxious to certain animals, a character which probably belongs to the dorsal glands (Hubbard, '03), which are very large and much more developed than elsewhere on the body. In this respect *Plethodon* appears to resemble *Triton cristatus*. (Capparelli '83.) However, the poison glands of *Plethodon* are not confined to the dorsum of the tail; much smaller ones are found on its ventral surface and also on the trunk and head of the animal, intermingled with mucous glands, which occur in all situations where the poison glands are found.

The principal question considered in the present paper concerns the changes occurring in the formation of the secretion and its expulsion from the glands. In *Plethodon* this involves the death of the glands, as Seeck ('92), Nicoglu ('93), Vollmer ('93) and others have shown for other Amphibia. The exhausted glands are here renewed or replaced in the manner described by

Heidenhain ('93 a), Vollmer ('93) and Nicoglu ('93). This process consists in the growth into the old glands of a new and smaller gland, which, however, is mucus in character, contrary to the statements of Nicoglu ('93), so that the poison glands develop from the mucous to the poison variety. This has been suggested but not definitely shown by Hoyer ('90) and Junius ('98), and distinctly denied by all other investigators of the regeneration of these glands. Under the histological structure of the glands will be considered some new points in the musculature, especially as to the presence in the epidermis of an apparatus for closing and opening the duct. The innervation of the muscles and epithelium of the glands will also receive attention.

This work was done under the direction of Professor C. A. Kofoid, and my heartiest thanks are due him for very kind assistance in every way and for criticism of results.

MATERIAL AND METHODS.

In order to obtain the best insight into the structure of the glands of the tail, sections in three planes have been made of that entire organ. The tissue was in all cases perfectly fresh and was fixed in Zenker's fluid, which has been satisfactory in all respects. Washing in 70% iodine-alcohol followed the use of the fixative.

That bony tissue might not hinder the passage of sections in any plane through the whole tail, the tissue was subsequently decalcified in a 5% aqueous solution of nitric acid for from twelve to twenty-four hours, followed by immersion in a 5% aqueous solution of sodium sulphate for the same length of time, and thorough washing in running water for from twenty-four to forty-eight hours.

Paraffine sections have alone been used, varying in thickness from $3\frac{1}{2}$ to 10 microns. The sections were fixed to the slide by the water-albumen method, and in all cases where possible staining was done on the slide.

A considerable variety of stains has been employed. The most successful have been Mallory's ('00) connective tissue stain (acid fuchsin, phospho-molybdic acid, anilin blue-orange G),

Van Gieson's haemalum and picro-fuchsin, and the iron-haematoxylin of Benda and Heidenhain. I have found it of considerable advantage to increase the percentage of fuchsin in Mallory's stain to as much as 1.5 or 2%. This stain, as a whole, when successful is very beautiful, but its action varies most unaccountably. The staining and differentiation will be perfect in some sections, while in others on the same slide the differential coloration will fail completely. But the range of application of the stain seems to be almost unlimited except for purely cytological work.

Other stains have been used, such as Mayer's neutral and acid haemalums followed by eosin, orange G, erythrosin and Congo red; safranin alone or in combination with light green; ferric chloride haematoxylin, and such special stains as the phosphotungstic acid haematoxylin of Mallory and Cajal's ('03) silver nitrate-pyrogallie acid method for nerves, Tänzer's orcein for elastic fibres, and Mayer's muci-carmin as a mucus stain.

As has been said, the largest poison glands of *Plethodon* are situated on the back of the tail, and in cross sections (Pl. XX, Fig. 1, *p.gl.*) it may be seen that they lie in that portion of the skin covering the dorsal half of the tail. Here the greatest development is in the glands at either side of the mid-dorsal line, while farther down on the sides they gradually diminish until they are considerably smaller and not readily distinguished by their size from the larger mucous glands. (Pl. XX, Fig. 1, *m.gl.*) The coloration also of the tail gives a clue to the location of the largest glands. The dorsal half of the tail is black or brown, while the ventral half is orange or yellow, and the glands under consideration are confined almost entirely to the darker portion. The mucus glands are found largely on the ventral side of the tail, but they also occur along the dorsal surface. In this region they lie between the necks of the large glands.

The poison glands form large sacs, extending from the epidermis to the inner layer of the corium. (Pl. XX, Fig. 1.) In shape they are elongated, with oval or even somewhat rectangular outline. The ducts are short, and the transition from the body of the gland to the neck and duct is not sharp as in the mucous glands, which are regularly flask-shaped.

It has been shown (Hubbard '03) that the swollen appearance of the tails of some animals is due to the increased development of the poison glands posterior to the well-marked constriction found just behind the cloaca in such cases. That this is really true appears in the study of a series of sections of a swollen tail passing from the tip up to and including part of the cloacal aperture. In the constriction the dorsal glands are very small comparatively, and are here no larger on the back of the tail than on the ventral side. But behind the constriction their development is much greater, and one may trace the regular increase in size as the series passes from the constriction back to the enlarged portion of the tail. Everywhere in the tail, except in the constriction at its base, the difference in size between the glands on the dorsal and ventral surfaces is maintained.

As is well known, the bodies of all the glands lie in a spongy connective tissue, the middle layer of the corium, which in the region of greatest development of the poison glands is increased enormously in thickness (Pl. XX, Fig. 1, *m.c.l.*), being alone from one-sixth to one-fourth or more of the dorsal-ventral dimension of the tail. (Hubbard '03.) The bottoms of the large glands rest upon or come very close to the inner layer of the corium. (Pl. XX, Fig. 1, *i.c.l.*)

The ducts of both mucous and poison glands pass through the outer corium layer and the epidermis, the long axis of the gland which passes through the duct and its mouth being perpendicular to the surface at the point where the duct opens to the exterior.

The histological structures found immediately surrounding the ducts of the poison glands are in no essential points different in *Plethodon* from those in other salamanders. The funnel cells and their processes (Pl. XX, Figs. 1 and 2, *f.c.*) are present as in *Triton* (Nicoglu '93) and in *Salamandra* (Ancel '02). The membrane-like structure lining the duct belongs to a specialized cell of the epidermis, corresponding to the "stoma cell" of Eberth. As Nicoglu has shown, the mouths of the glands lie within these cells, processes of which extend down in the ducts about as far as the lower limit of the epidermis or a little farther. (Pl. XXIII, Fig. 27, *p.f.c.*) The prolongations stain black in iron haematoxylin, reddish in Mallory's and yellow in Van Gieson's stain.

In addition to the funnel cells proper, Nicoglu has described the arrangement of the cells in the epidermis which are to replace the funnel cells as they are thrown off at the time of moulting. The same condition is found in *Plethodon* and does not differ at all from that in *Triton* (Nicoglu '03) or in *Salamandra* (Ancel '02). (Pl. XX, Fig. 4; Pl. XXIII, Figs. 27, 28, 29, 30. *rep. c.*)

As further evidence that the cells described as replacement cells really have that function, *Plethodon* shows that the lower ends of the replacement cells, especially those nearest the duct, extend inward as do the prolongations of the funnel cells. (Pl. XXIII, Fig. 27, *rep. c.*) The arrangement of the former very strongly suggests that they are of the same nature and function as the funnel cells. And in cross sections of the ducts the replacement cells are shown rolled one within the other as in Pl. XX, Fig. 4; Pl. XXI, Fig. 16, *rep. c.* The cell first to replace the one thrown off at moulting immediately surrounds the duct; the cell next to replace this one lies concentrically outside it, and so on. In Mallory's stain the cell boundaries are very distinct, and there can be no doubt of the structure as described either in cross or in longitudinal section of the ducts.

The walls of the gland sacs proper are composed, in many *Amphibia*, of a number of elements which have been described and all of which need not be discussed at length here. In the most peripheral layer are connective tissue and elastic fibrils, as is shown by the use of Mallory's connective tissue stain for the former and orcein for the latter. Nerves, lying in this layer, also extend over the gland. Inside the connective tissue sheath, as it is generally called, lie the muscle fibres, and next to them the epithelium of the gland.

(See in this connection Drasch '92, '94; Eberth '69; Eekhard '49; Englemann '72; Hensehe '56; Leydig '76, *a, b*; Paulieki '85; Phisalix-Picot '00; Schuberg '03; Schultz '89; Seeek '91; Stieda '65; Tonkoff '00; Wiedersheim '86.)

Because of the intimate relation between the connective tissues of the gland wall and those of the corium, it is necessary to consider in more detail the structures of the inner, middle and outer layers of the corium. Schuberg ('03) has studied the corium of *Axolotl* most minutely. I have confirmed his results

in general in *Plethodon*, and particularly as to the relation of the connective tissue bundles of the inner layer of the corium to those of the middle layer. He found (p. 222) that columns of connective tissue pass perpendicularly from the inner into the middle layer, and seem to serve as mechanical supports for the glands, since under each one such a column of tissue is found. The same arrangement occurs in *Plethodon* except that the perpendicular bundles do not stand beneath the glands, but around them, as can be seen in longitudinal sections of the glands. (Pl. XX, Fig. 5, *c.t.b.*) In spaces between the large glands or on the ventral side of the tail, the bundles from the inner layer of the corium can be seen especially well. The connective tissue fibres from the wall of the gland unite with the outer layer of the corium which then, lying next the muscle layer of the gland, passes toward the surface of the epidermis and ends on the side of the neck of the gland about a third of the distance between the inner and outer boundaries of the epidermis. (Pl. XX, Fig. 8; Pl. XXIII, Figs. 27, 31.) This appears in both longitudinal and cross sections of the ducts. In the latter can be seen a crescent of connective tissue on each side of the duct between the muscle fibres and one of the replacement cells. (Pl. XXIII, Figs. 28, 29; Pl. XXI, Fig. 16, *c.t.*) Ancel ('02, Pl. IX, Fig. 22) seems to have shown the same in longitudinal section.

The elastic fibres pass through the inner layer of the corium into the middle layer in company with the connective tissue bundles as Schuberg ('03, p. 231) has described. The elastic fibres can be followed around the glands, and over them in tangential sections. The fibres are of nearly the same calibre throughout and all of them take the same general direction, from the inner corium layer perpendicularly or sharply turned toward the outer layer. As in the case with the connective tissue bundles the elastic fibres pass at once around or over the large glands, and are not found arranged perpendicularly beneath them as in *Axolotl*. (Schuberg '03, p. 232, Fig. 14.) On the surface of the gland they are branched in a few cases; usually, however, only single fibres of wavy, curving and regular outline are visible, ending before the outer corium is reached (Schuberg '03, Pl. XXI, Fig. 9, *el.f.*).

Between the connective tissue layer and the gland epithelium lies the layer of contractile or smooth muscle fibres. These were first shown histologically by Hensehe ('56), though before him Ascherson ('40) had observed movements of the living glands. Since this time there has been no doubt of the existence of muscles in the walls of the poison glands (Coghill '99; Drasch '89, '92, '94; Eberth '69; Eckhard '49; Englemann '72; Heidenhain '93 *a, b*; Leydig '76, *a, b*; Massie '94; Nieoglu '93; Paulieki '85; Phisalix-Pieot '00; Schultz '89; Seeek '91; Stieda '65; Szezesny '67; Vollmer '93). As regards the smaller series of glands the question seems to be open. The absence of contractile fibres on them has been used as a character to separate them from the large glands. The muscles of the large glands are arranged in a single layer and have a general meridional direction on the gland, converging toward the upper pole. The fibres are usually simple but may be branched (Pl. XX, Fig. 7); this occurs mostly on the lower part of the gland. Neither do the muscles form a continuous sheet about the gland; the individual fibres are separated by spaces of greater or less extent. I have not been able to find with certainty muscles on glands which are mucous in nature.

The nuclei of the contractile cells, contrary to the description of Nieoglu ('93, p. 437,) and such figures as his and those of Vollmer ('93), lie in the upper region of the glands just outside the uppermost gland cells, yet still well beneath the epidermis (Pl. XX, Fig. 6; Pl. XXIII, Fig. 31, *m.n.*). The first observer mentioned has shown (his Pl. XXII, Fig. 12) the nuclei of the muscle cells in *various locations about the periphery of the glands*; but in *Plethodon* the nuclei have a constant position as described and are found only there. In the region of the nuclei the muscle fibres are considerably larger than elsewhere on the gland, as is shown in Pl. XX, Fig. 8, *m.f.*, or Pl. XXIII, Fig. 31, *m.f.*, so that the muscle, especially in longitudinal sections of the glands, seems to bear a flask-shaped expansion. From this point it is possible to trace a single fibre very nearly to the base of the gland, and also outward around the neck of the gland into the epidermis. (Pl. XX, Fig. 6.) The connection of the muscles with the epidermis has been reported by Nieoglu ('93) and Heidenhain



('93 b), and the arrangement in *Plethodon* is a similar one except as regards the presence of the "Schaltstück" cells described by them. In *Plethodon* the "Schaltstück" is not demonstrably present except in one or two questionable cases in all my preparations, and Vollmer ('93) found that it is very often absent even in *Triton*. There can be no doubt, however, that the muscles send processes into the epidermis. This is especially well shown in longitudinal and cross sections of the ducts.

The statement that the muscle nuclei of the poison glands in *Plethodon* lie only in the necks of the glands, instead of generally distributed about the periphery as held for other animals, may be supported by several facts. In the first place, longitudinal sections of the glands through the duct and mouth show two nuclei, one at each side of the gland where the sac begins to pass over into the duct. In sections of the same plane which pass a little to one side of the duct (Pl. XXI, Fig. 10, *mf.*, *mn.*) may be seen in some cases the obliquely cut ends of as many as seven muscle cells each with its nucleus in situ, and occupying exactly the position relatively of the two lateral nuclei which are shown in the median section. There can be no doubt of their structure.

Cross sections of glands and ducts are also very instructive on this point. In such, especially if stained in Van Gieson (Pl. XX, Fig. 12), there are shown in many cases the light yellow muscle fibers between the gland cells and the connective tissue, when the plane of the section passes more deeply through the gland than the position of the nuclei of the muscles. But when the gland is cut across at the level of the nuclei, the evidence gained from longitudinal sections is even more strikingly upheld. In such cross sections can be seen as many as twelve or fourteen muscle fibres stained light yellow (in Van Gieson), and in very sharp contrast to them the brown or black nuclei. And in this region the section of the muscle is larger than it is deeper in the gland; this corresponds to the flask-shaped enlargement seen in median longitudinal section (Pl. XX, Fig. 8, *mf.*). If a series of frontal or cross sections of the tail is studied, it will be found that while the muscles themselves can be traced until the bottom of the gland is reached, nuclei never appear again which are unmistakably those of the muscle fibres. The only place in

which one can be sure that he is dealing with nuclei of the contractile fibres is in the location above described. Hundreds of sections have been carefully examined and there has never been a case of a fully formed gland in which the muscle nuclei are situated in any position except that described. Not only is this true in stains such as Mallory's and Van Gieson's but also in clear nuclear stains like iron haematoxylin.

That those observers who describe muscle nuclei on the periphery of the gland sacs have mistaken connective tissue nuclei for them, seems to me very probable. Nicoglu ('93, p. 438) says that the nuclei often occupy an eccentric position, so that even with oil immersions one cannot see that there is any protoplasm of the muscle cell about them. His description ('93, p. 436) of the flattened narrow nuclei of the muscle cells applies more to connective tissue nuclei. That these occur in the walls of the glands has been observed by Paulicki ('85, p. 158), who says: "An die Drüsen treten gewöhnlich . . . sich nach oben erstreckend bindegewebige Stränge mit Kernen." And the figures of Schuberg ('03), especially Fig. 28, show that this is true for the glands of Axolotl. From these facts and from my observations on *Plethodon* it is clear that connective tissue nuclei closely invest the glands, and evidence is added to that already brought forward to show the location of the nuclei of the muscle cells.

The processes of the muscles passing into the epidermis serve to connect the fibres with the outermost layer of the skin. This has been shown, as said before, by Heidenhain ('93) and Nicoglu ('93), as well as by Ancei ('02), and there is nothing to be added to the description given by the former except, as before stated to mention the frequent non-occurrence of the *Schaltstück* as such. This is a structure described as containing about four cells which are arranged in a ring about the neck of the gland at the lower boundary of the epidermis. The cells form seemingly the principal points of insertion of the muscle fibres, but this cannot be so in *Plethodon* where the *Schaltstück* is virtually absent. Otherwise it may simply be said that the upper or outer ends of the muscle fibres pass into the epidermis and end between the replacement cells of the funnel. This can be seen fairly

well in cross sections of the gland ducts in the epidermis where the cut ends of the muscles are seen close beside the funnel cell (Pl. XXIII, Figs. 28, 29, *prol. m.f.*). In good longitudinal sections of the ducts the muscles (Pl. XXIII, Fig. 27, *prol. m.f.*) are seen to end between the older replacement cells which are already elongating into their typical form (same, *rep. c.*). Nicoglu ('93) represents the endings as between the cells, but Aneel ('02) seems to consider them as special parts of cells. At any rate he has shown (Fig. 22) the fibrils as within cells in the epidermis. I have not been able to find such structures as he shows; there can be hardly any doubt that the prolongations of the gland muscles into the epidermis end between the replacement cells. Nieoglu and Heidenhain ('93) and Aneel ('02) have remarked upon the existence of intercellular bridges between the muscle cell on the one hand and ectodermal epithelial cells on the other, as Nicoglu says (p. 440), "von ganz ähnlicher Art wie zwischen den Oberhautzellen selbst."

I have not found the intercellular bridges in *Plethodon* between epithelial and muscle cells, but all the facts concerning the connection of muscle and epidermal cells have been taken as evidence of the ectodermal origin of the muscles of skin glands. This has been so often commented upon that it is useless to more than call attention to it here. The evidence gained from a study of the development of the glands shows that the muscle fibres come from the Malpighian layer of the epidermis (Aneel '02; Vollmer '93; Junius '98). This, added to the facts already cited, and coupled with the observations of many investigators (Engelmann '72; Seeck '91; Heidenhain '93; Nicoglu '93) seems fairly conclusive that the muscles of the dermal glands are of ectodermal origin: (Compare also in case of sweat glands, v. Kolliker '89; *Handbuch des Gewebelehre des Menschen*, pp. 138 and 258).

The existence of a sphincter or constrictor muscle for the glands has been claimed by Schultz ('89), who described a band of muscle fibres running around the neck of the gland beneath the meridional layer. This observation has been disproved by Drasch ('94) and Nicoglu ('93), and I have been unable to find such a structure in *Plethodon*. And there is no evidence of the

epithelial plug of Draseh ('94) for restraining the contents of the gland under pressure. Phisalix-Picot ('00) mentions (pp. 44-45) an orbicular muscle, but gives no description or drawing of it, so that her meaning is obscure. Dilator muscles for the ducts or mouths of the glands have never been described.

However, both dilator and constrictor muscles occur about the mouths of the poison glands of *Plethodon*. These are best shown in sections of the epidermis parallel to the surface, stained in Mallory's connective tissue stain, which are, of course, also cross sections of the ducts. All three sets of gland muscles may very often be seen in one such section (Pl. XXIII, Fig. 30, *con. m.*, *dil. m.*, *m.f.*; Figs. 28, 29 also). In these cases it will be seen that the duct (*l.d.*) in the epidermis is oval in cross section, and that at each end of the oval is a triangular mass of fibres, staining red in Mallory, as do the muscles on the body of the gland. The fibres converge toward the duct and insert upon the replacement cells nearest the funnel in such a way that by contracting they will bring the lips of the duct together and so close or greatly diminish its lumen (Pl. XXI, Fig. 16). The constrictor fibres are differentiations of the cell whose large nucleus (Pl. XXI, Figs. 14, 16; Pl. XXII, Fig. 28, *nuc. ep. m.c.*), stands at the ends of the elliptical opening of the duct. The fibres lie within this cell as can be especially well seen in longitudinal sections of the glands which do not pass through the duct. Here it appears that the cell of which the constrictor fibres are a part, together with its nucleus, lies in the deepest layer of the epidermis immediately upon the outer layer of the corium. This cell seen in surface view is equal in extent to several of the neighboring epidermal cells, but in cross section it is very much flattened (Pl. XXI, Fig. 13). Anceel ('02) has figured such a cell, but gives no clue as to its function.

The dilator fibres belong to the same cell of which the constrictors form a part, and are at a slightly lower level seemingly than the latter. The action of the dilator is two fold. Some fibres pass around the ends of the oval opening of the duct (Pl. XXIII, Fig. 28, *dil. m.*; Pl. XXI, Fig. 14) and when they shorten they tend to separate the lips of the lumen more widely, by pressing at the ends of the ellipse. This is evident when it

is seen that the mass of dilators is often concave in outline toward the center of the duct (Pl. XXIII, Fig. 28; Pl. XXI, Fig. 15, *dil. m.*), so that in contraction the fibres first mentioned pull in the general direction of the major axis and toward the center of the ellipse. Other dilator fibres attach at the edges of the duct near the end (Pl. XXI, Fig. 14), and in shortening pull in the direction of the minor axis of the ellipse, thus widening the lumen by spreading its walls at the tips of the oval. (Pl. XXI, Fig. 14.) The entire effect of the dilator fibres is to make the aperture of the duct nearly circular, thus offering freer exit to the secretion. Their action would be to open the duct from the form shown in Pl. XXI, Fig. 16, to that, for example, in Pl. XXIII, Fig. 30.

The fact that the constrictor and dilator fibres lie entirely within the epidermis need not militate against their having the function of muscles, for in the case of the intrinsic gland musculature it has been well established that it has an ectodermal origin. It is certain that the arrangement and appearance of the fibres described as constrictor and dilator muscles are such as to suggest very strongly both that nature and function. The coloration in Mallory is exactly that of the smooth muscles of the glands; and the convergence of the constrictor fibres to their insertion in a position where contraction would close the duct; the endings of the dilators in places to be of greatest advantage in widening it when the muscles contract—all these facts lead one to conclude that he has to deal with an apparatus for closing and opening the ducts of the glands.

The muscles of the poison glands, as has been said, immediately envelop the secretory cells. The entire gland is filled with enormous cells, the generally recognized "Giftzellen" of many authors or the "giant cells" of Leydig. In such glands a lumen does not exist; this is especially well shown in sections of the tail of a tadpole 38 mm. in length, in which the cell boundaries are distinct, the secretion not yet being present in sufficient quantities to obliterate them. There it will be seen that the ends of the cells are in contact with the middle of the gland, thus doing away with any trace of a lumen (Nicoglu '93; Seeck '91; Calmels '83). A glance at the figures will serve to distinguish

in this respect the poison and mucous glands; the latter have capacious lumens (Pl. XX, Fig. 2), often filled with a clear secretion. The large gland cells each have a number of nuclei (Nicoglu '93; Draseh '92), not over four in *Plethodon*. They are round or oval, of regular outline, and lie normally upon or very near the wall of the gland, and so at the base of the cells. The internal structure of the nuclei is simple. There is a scanty network and few chromatin granules; usually also one or two nucleoli.

The cells and nuclei of the small or mucous glands are distinct in every way from those of the poison glands. The cells are low and cubical and show a filar structure (pseudo-filar, Nicoglu '93). This is seen in sections stained either with Van Gieson, Mallory or iron haematoxylin. The nuclei are smaller than those of the poison glands, and angular instead of regular in outline. They invariably stain intensely black in iron haematoxylin, remaining so when the nuclei of the giant cells have decolorized to a very faint gray (Pl. XX, Figs. 2, 3; Pl. XXII, Figs. 18, 19, 20).

A general comparison of the two sorts of glands might be instituted in some such terms as these. The poison glands are very much larger than the mucous glands, and have contractile walls; the mucous glands lack this character. The extreme dimensions of the former on the tail are approximately from 1400 microns in length and 380 microns in breadth to 680 microns in length by 200 microns in breadth, and half the latter figures on the body. The mucus glands vary from 93 by 90 microns on the tail to 60 by 40 microns on the body. This alone, without closer inspection, would serve to generally distinguish the two varieties of glands; but in addition the poison glands have no lumina, the cells and nuclei are much larger than in the other glands (mucous average about 11 microns in greatest diameter, poison about 20 microns) and stain differently; and above all the character of the secretion is vastly different.

As might be gathered from the name often applied to them, the secretion in the poison glands is composed of granules. These are of varying size, and the cells are entirely filled with them. The mass stains from red (Pl. XXIII, Fig. 31, *sec.*) or reddish yellow to a dark purple in Mallory; in Van Gieson the

color is as a whole yellow with a tinge of red. In iron haematoxylin some granules stain (Pl. XXII, Fig. 18) black; but at times one can detect in some granules a clear outer portion which takes the counter stain (erythrosin, etc.), while the central part stains dark black, and others which take only the counter stain.

The mucous secretion, on the other hand, reacts very differently, as does the cytoplasm of the mucous cells, which can be easily distinguished from their secretion. Here the reactions are typically those of mucus. Mallory's stain, which colors mucus in the sublingual of a cat a clear blue in two minutes, stains in the same way both the cells and the secretion of the small glands. This same stain beautifully differentiates the mucus in the goblet cells of the oesophagus and intestine of *Plethodon*. I have not been able to obtain the reaction in these gland cells with thionin, in which Nicoglu places so much confidence as a mucous stain. Hubbard ('03) has had the same difficulty. However, mucicarmine, a specific mucous stain, gives the mucous reaction after twelve or twenty-four hours in both the glands of *Plethodon* and the sublingual of the cat. The use of Van Gieson's stain clearly differentiates the small gland from the large ones. In the former the cells and the secretion are stained a clear red or pink, without a trace of yellow as in the poison glands. Orcein also, which has been described as a mucous stain, colors the cytoplasm of the mucous gland cells a deep brown, and has absolutely no effect on the granular secretion of the poison glands. The iron haematoxylin is of little use in revealing the mucous nature of the small glands, since they take only the counter stain except for the nuclei. These become a deep black as already said. But this method at least serves to distinguish the two sorts of glands aside from the nuclear staining, in that the secretion of the small glands never takes the haematoxylin, as do the granules of the large glands.

From these distinctions as to the primary character of the two classes of glands, we are led to consider the histogenesis of the secretion. It has been generally held that this process is not the same in the mucous and poison glands. Seeck ('91), p. 55, holds that the secretory cells are of two sorts, "solche die als

Zellen erhalten bleiben und Drüsensecret secerniren (Schleimdrüsen), und andere, deren Protoplasma sich in feinkörniges Drüsensecret metamorphosirt wobei die Zellen vollkommen aufgebracht werden, zu Grunde gehen, so dass man ihre in Zerfall begriffenen Kernen in Drüsensecret finden kann (Körner-oder Giftdrüsen)." Nicoglu ('93), p. 447, finds that the cells of the poison glands "wenn ihre Stunde gekommen ist, wandeln sie sich in toto in Secretmasse um." But up to this time they act as other gland cells in elaborating and retaining a secretion in their interior, as the pancreas cells do zymogen granules. Schultz ('89) does not think that all the cells of a gland are destroyed at the same time, but such as do form a part of the secretion mass must be regenerated; indicating that they are destroyed in the process of secretion. Drasch ('94) merely states that the poison glands of the salamander, if completely emptied, pass entirely away, and are replaced by new glands. Observations of the glands at various times after emptying show regressive changes in all the layers. Vollmer ('93) also has described the process of solution of the Leydig cells after strong electrical stimulation of the glands, and has made careful statements regarding the appearance of the emptied glands. The conditions in *Plethodon* almost duplicate those he has described.

It seems pretty well founded, then, that the poison gland cells pass bodily into the secretion mass. But a distinction should be made here, as Nicoglu has done, between the secretion mass as that thrown out, and the secretion material, which is the formed substance in the cells. There is no evidence of the disintegration and solution of cells in the full but not discharged gland. It is only when for some reason the glands are emptied that the degenerative processes are discerned. Otherwise the formed secretion is retained within the cells, which remain in a normal condition at such times.

This review of the literature describes very well the processes which go on in *Plethodon*; Pl. XXI, Fig. 17, will show the appearance of a gland on the day it was emptied. It has shrunk greatly in size; as compared with others of the same animal which, for some reason were not emptied, from three hundred microns in diameter, say to one hundred microns. The



nuclei which in full glands lie at the bases of the cells, are in this case in the inner parts of the cells, and are larger and clearer and in a state of disintegration. In some places only outlines or shadows of nuclei can be seen. Often they became shrunken and irregular in outline when the gland is emptied. The entire appearance of emptied glands would lead to the conclusion that their time of functional activity is at an end.

The mucous glands, on the other hand, never reveal such changes. It seems correct to say that the processes there are like those in milk glands, where parts of the cell bodies are thrown off as secretion, while the remaining portions in time repeat the same processes of secretion. Nussbaum ('82, p. 302) speaks of the heads or inner portions of the mucous gland cells of Salamander as discharged on stimulation.

If it is true then, as it seems to be, that the poison glands are changed bodily into the mass of secretion, we must look to some source for their replacement, if the animal is to have their continued protection. Nussbaum's conclusions should be cited here ('82, p. 336) as bearing on the general topic of death of gland cells through secretory activity, and their renewal. He says secretion consists in the formation and elaboration of the mother-substance of the secretion material, the changing of this in the cells and in emptying the secretion when ready, out of the cells. "Wie alles Lebende aus uns unbekannten Ursachen abstirbt und neuen Generationen Platz macht, so gehen auch nach einer gewissen Zeit Drüsenzellen zu Grunde und werden von lebenskräftigen Nachbarzellen ersetzt. Sterben aller Zellen gleichzeitig ab, so ist die Drüse vernichtet wie eine Protozoen Colonie. . . . Die Secretion mag wohl die Zelle abnützen; die Zelle wird altern. Der Ort der Secretion ist aber nicht gleich bedeutend mit Zellentod; er ist eine energische Lebensthätigang."

In this particular case of the skin glands of Amphibia, a definite process of replacement goes on, occurring in *Plethodon* in the way described for other salamanders by Nicoglu ('93), Heidenhain ('93) and Vollmer ('93), and not as Junins ('98) claims, by entirely new origin. The former observers find that inside the old poison glands there lies a second smaller gland, possessing a lumen. This small sac is to replace the older gland

and lies always between the musculature and epithelium of the latter. Nicoglu ('93) finds that the new glands possess "all the epithelial parts of the old gland with the exception of the "Schaltstück." Whether this statement is to include also the muscle fibres, he does not say; his figures show muscle cells lying upon the ingrowing gland, but there is no reference to prove that they belong to it rather than to the old gland. However, Vollmer ('93) says that the new gland contains both gland cells and smooth muscle fibres, which arise as does the gland bud, from the Malpighian layer of the epidermis.

The place of origin of the replacement glands is found by Nicoglu ('93) and Heidenhain ('93a) in the very small, flattened cells immediately adjoining the Schaltstück and lying inside the gland. Vollmer ('93) on the other hand concludes that the place of origin of the new gland "ist das Keimlager des Rete Malpighi. Auch die von Heidenhain erwähnten unscheinbarer Zellenelemente, denen er die Bildung der Drüsenknospe zuschreibt stammen vom Rete Malpighi." There is no reason, he says, why the new glands inside the old ones should not differentiate as do the first glands in the course of their development.

In *Plethodon* the method of renewal of the worn-out glands is as these authors have described, but there is no evidence showing the source of the replacement glands, and the subject must be dismissed with the above references to the literature.

But whatever the source of the new glands, there can be no doubt that in every old gland without exception there is a small sac or replacement gland. This is always found in those glands which have not been discharged (Pl. XXIII, Fig. 31), as well as in those which have been and show the most extensive degenerative phenomena. In this respect *Plethodon* seems to differ from *Triton* (Vollmer '93). This author states that the growth of the new gland is initiated when the old glands are emptied. Nicoglu ('93) mentions the fact that the old poison glands contain the smaller sacs, but does not say definitely whether or not the destructive processes must have set in before the new gland makes its appearance. But in *Plethodon* the *presence* of the replacement gland is not dependent on the secretory processes in the large glands. The former are present in the glands of an

animal thirty-eight mm. long which are not filled with secretion.

We have to deal then, in these cases, with the regeneration of a gland by a gland. Individual cells are not broken down, and then renewed by the growth of new cells as Schultz ('89) maintains, and as seems to be implied by Calmels ('83), who finds that the young gland cells are indifferent elements which may develop into either poison or mucous cells, so that a gland may be poisonous only in part.

The question, however, as to whether a poison gland is replaced only by a poison gland is still to be considered. May not these be renewed by glands which to begin with are mucous in character? That is, may not a specific poison secreting epithelium be replaced through mucous cells, and gland by gland instead of cell by cell? These inquiries have been raised by Nicoglu, and he says ('93, p. 425) that a mucous cell never goes over into a poison cell, or vice versa, and Schultz ('89) also says that mucous glands are always only mucous glands, and poison glands only poison glands (p. 33), and therefrom we are to suppose that the same is true of the individual cells, as he finds that cells replace cells.

Still the evidence gained by a study of the poison glands of *Plethodon* indicates rather strongly that we have to deal with *a production of poison glands from mucous glands entirely*. Nicoglu has already shown that in *Triton* a mucous gland may sometimes replace a poison gland entirely, but he very strongly opposes the idea that the function of such a gland ever changes. He holds (p. 435) that the condition of mucus within poison gland is a functional adaptation, because the animal needs more mucous glands than are on hand. Everything goes to show that in *Plethodon*, on the other hand, the occasional method of regeneration described by Nicoglu is the only one. The replacement glands already described stain blue without exception in Mallory, which has been shown to be a mucous stain. The contrast between the blue of the mucus and the red of the granular secretion is very sharp (Pl. XXIII, Fig. 31). The mucous reactions described for Van Gieson, orcein and mucicarmine, are shown invariably in the replacement glands as in the mucous glands outside, and the correspondence of the replacement

glands stained in iron haematoxylin with the other mucous glands is just as complete (compare Pl. XX, Figs. 2 and 3).

There can be nothing clearer than the reaction of the new glands to Mallory's stain. The blue color is present in every case as shown by a study of hundreds of glands. In the very large glands on the back of the tail the ingrowing glands never reach beyond a certain size, such as is shown in Pl. XXIII, Fig. 31. This may possibly be due to some effect of the poison which would hinder the growth of the small gland, or, as seems more likely, the new gland does not develop because it is hemmed in and hindered in its growth by the pressure of the large amount of secretion in the old gland. Drasch ('94) has made this suggestion previously, but does not say where the replacement glands are located. But in all the small poison glands which lie along the sides of the tail and also on the dorsal and ventral surfaces, particularly in the constriction, can be seen all stages of development of the mucous glands within them, from the small buds to new glands which have almost entirely replaced the old ones. The small poison glands differ from the largest ones in no other respect than in size, and for that reason it seems fair to conclude that the processes of regeneration going on in them are characteristic, and typical of those believed to occur under certain circumstances in the large glands of *Plethodon*, and as observed in other salamanders. There are many cases to be seen in *Plethodon* in which some glands are so far replaced by a new mucous gland that only a faint crescent of granular secretion can be seen, the rest of the contents being mucus. In other cases the amount of granular material is a little greater, and in still others we may see the gland half granular and half mucus (Pl. XX, Fig. 3; Pl. XXII, Figs. 18, 19, 20). In all these the granular portions stain as do the same parts of the large glands, while the remainder reacts to Mallory and the other stains as do the small sacs in the large glands and the mucous glands outside of these.

To sum up the foregoing we may say that the small glands within the large ones react like known mucous glands to Mallory's stain and mucicarmine, and in the same way so far as the nuclei of the replacement and mucous glands of the tail are concerned,

to iron haematoxylin. That is, both the mucous cells and those of the replacement glands stain blue in Mallory, red or pink in Van Gieson, and both have a fibrillar structure. The mucous reaction is also given with mucicarmine. And finally, the nuclei of the ingrowing gland fundaments always stain intensely black in iron haematoxylin, as do the nuclei of the mucous glands.

The facts just related have been gained entirely from a study of preparations made from material taken from unstimulated animals, that is those not irritated prior to immersion in killing fluids. The evidence along this line is stronger and more convincing in the case of an animal which, without stimulation of any kind other than such as might have occurred in nature, got rid of a great deal of the secretion in the glands of the tail and then cast that organ off, as if it could be of no further use. The animal in question, when first observed, was seen to be entangled head down between some pieces of bark in the terrarium in which it was confined. This seemed to irritate the salamander very much, for when it freed itself it began moving quickly about, swinging its tail from side to side like an angry cat. The tail, during this time, became covered with a very abundant white secretion. After about five minutes of such behavior on the part of the animal, when I merely touched the tail it was suddenly thrown off, the break being in the constriction back of the cloaca.

The tail was put into Zenker's fluid after about fifteen minutes, and sections made later. Here the likeness between the fundaments in the empty poison glands and the mucous glands could not be more complete. In all the stains used the appearances are exactly the same. The cells of the mucous glands are much higher than in other animals seen, stain a lighter blue in Mallory, and have a vesicular structure approaching granular, rather than the filar structure usually seen. Even so, the replacement glands cells are their exact counterparts, and show the same reactions to Van Gieson, mucicarmine, and iron haematoxylin, as well as Mallory's stain.

It seems hardly possible that the cells of the mucous glands could have so changed their structure and appearance in fifteen or twenty minutes, though the increase in height and consequent

diminution in size of the lumen of the gland, together with the vesicular structure of the cells, would lead one to think that they are in the way of becoming granule or poison cells. But whatever the interpretation put upon this appearance, and to whatever source it is due, it must be admitted that the fundamentals in the old poison glands have undergone the same processes and their histological characters are now exactly similar to those of the mucous glands.

Further evidence that the glands are originally all of the same character may be gained from the literature. Ancel ('02), who has followed very closely the development of the skin glands in salamander, considers that the large glands represent organs more completely differentiated than the small glands toward a special functional adaptation, though both in early development are absolutely alike (pp. 269, 283.) Junius ('98) believes that there is but one kind of gland in the skin of the frog and probably of all Amphibia, and that the various glands of the authors are young and old forms or developing stages of them. He says further that in the frog he has not seen the regeneration described by Vollmer and Nieoglu, and declares that atrophied glands are replaced by wholly new ones developed by downgrowths of epiderm cells into the cutis. According to him, small glands represent young stages of large ones, and the former are equivalent to the non-contractile or mucous glands, while the latter are the dark, contractile, granule or poison glands.

Again, Hoyer ('90, p. 354) finds that in some poison glands of the salamander single cells or groups of cells lying between the non-staining large granular cells take on a red-violet color in thionin (which he employs as a specific mucous stain). He makes the suggestion merely: "Möglicher Weise deutet dieses eigenthümliche Verhalten auf eine genetische Beziehung der in den Drüsenzellen enthaltenen mucinähnlichen Substanz zu dem giftigen Secrete." And finally, the observation of Phisalix-Picot ('00) that the secretion of the mucous glands of the Salamander is poison, seems to me to bear along this line of a correlation between the so-called mucous glands and the poison glands.

Evidence in this direction also, further than that already advanced seems to be indicated in the poison glands of *Plethodon*.

Here there is very frequently a distinct blue tinge to the *granular* secretion. This may possibly be because the metamorphosis from "a mucus-like substance to the poison secretion" is not entirely completed. At any rate one is impressed with the likelihood that there is mucous material in the poison glands outside of that contained in the replacement glands.

In the discussion of the replacement of the poison glands by those of the mucus variety, it has been shown that every large gland has within it the fundament of a new gland which to all stains for mucus except thionin gives the mucous reaction, and which is also the exact counterpart of the small glands having the mucous secretion. The fact that only in poison glands of smaller size are found evidences that they are entirely replaced by mucous glands, may be explained on the ground that there the amount of granular secretion is not sufficient to mechanically hinder the growth of the new replacement gland. The actual transition stages from mucous to granular secretion have not been observed in my material.

If we make the assumption in view of these facts that the glands of mucous character in the poison glands develop only into mucous glands on the death of the latter, we are forced to one of two conclusions: either that the small glands *outside* the large ones, especially in *Plethodon* on the dorsal surface of the tail, become the poison glands, or, on the other hand, that when the latter are once destroyed there is no return to such structure except by developing anew according to the embryonic type.

The latter process is going on continually in large as well as in small animals, as can be readily seen by inspection of sections. But it seems that the fundaments are all alike to begin with (Ance! '02); as this author says, the solid gland buds in which a cavity is formed do not undergo further important morphological transformations, and constitute the mucous glands. Those which remain solid, however, continue their development in other ways and form the poison glands (p. 269). It seems to me that this is equivalent to saying that in embryological development the poison glands pass through a mucous stage to reach their final form and character. It certainly lends evidence to the view

expressed, that the glands which are to replace the worn-out poison glands are originally mucus in character.

There is no reason to believe, however, that the replacement glands are functionless during the life of the poison glands in which they lie. Even the smallest replacement glands have distinct ducts and epithelium, and in some cases it is absolutely certain that they have elaborated a secretion similar in every respect to that of the mucous glands.

It is very probable that under all ordinary conditions the small glands in the large ones secrete mucus, and in this sense are adaptations; not because the animal through some unusual external conditions has come to need more mucous glands as Nicoglu ('93) says, but rather because under normal environment there is always need of more mucus than can be secreted by the glands outside the poison glands, especially when the latter are so closely crowded together as on the back of the tail in *Plethodon*. And much evidence goes to show that under stress of necessity such mucus secreting glands become by replacement the more highly specialized poison glands and take on a particular function, that of forming a substance protecting the animal from its enemies (Hubbard '03.)

The nerve supply of the skin of *Amphibia* has been a favorite subject of study for many years. Most investigators have limited themselves to the terminations in the sense organs of the skin and in or on the ordinary epidermal cells (Pfitzner '82; Canini '83; Frenkel '86; Massie '94; Herrick and Coghill '98; Coghill '99). The innervation of the glands has received less attention.

Eckhard ('49) first showed that the glands could be emptied by stimulating the anterior roots of the cerebro-spinal nerves, but did not consider the structure of the nerve endings. Eberth ('69) found that there is a network of very fine fibres close upon the glands; Englemann ('72) came to the same conclusion and showed farther that from the nerves about the gland fine twigs are given off to the contractile cells. Openschowski ('82) describes a network of nerves surrounding the glands, as well as an intracellular net; but from his figures it is hard to believe that the structures he shows are nerves. Drasch ('89) also experimentally proved the efficacy of nerve stimulation in obtaining

secretion from the glands, as does Phisalix-Picot ('00). Eberth and Bunge ('92) have described free nerve fibres which seem to end with knobs outside the epithelium of the ball of the thumb of the male frog. Loeb ('96) has also shown how closely the glands of *Amblystoma* are connected with the central nervous system. In 1898 Herrick and Coghill were able to show the existence an intimate connection of nerve fibres with the walls of the glands, but were unable to discover the exact relation of the fibres to the gland cells. They also described the plexus of nerves beneath the corium as being composed of two sorts of fibres; larger ones connected with the nerve bundles of the central system, and smaller ones which in part, at least, originate in ganglion cells in the corium. Schuberg ('03) has criticised the results of these authors, contending that many or all of the nerve bundles described are really connective tissue bundles, and that the ganglion cells are the "Mastzellen" he himself figures.

Massie ('99) continuing the work of Herrick and Coghill, considers the same arrangement of fibres beneath the corium, and also shows that nerves end on the muscles of the "ental" glands. He finds that nerve fibres passing from the nerve bundle plexus under the corium are intimately connected with the ental glands, and seem distinct from the nerves supplying the muscles. "It seems, therefore, that there are two groups of nerves passing to the glands of the ental series; the one attaching by the typical endings to the enveloping muscle cells, the other ramifying promiscuously over the surface of the gland." (p. 59.)

In the study of the nerves of the poison glands of *Plethodon*, three methods have been relied upon; namely, the silver nitrate-pyrogallie acid method of Cajal, and Mallory's phosphotungstic acid haematoxylin and fuchsin-orange G-anilin blue methods. The last named gave most excellent results, while of the other two Cajal's was only indifferently successful.

The haematoxylin of Mallory stains only the sheaths of the nerves and so it is of no value in tracing the axis cylinders, since, as is well known, the nerves lose the medullary sheaths on passing into the corium. Beneath the corium, however, the nerves can readily be followed by this method. In some instances fibres

are shown running for long distances beneath the corium, and branches can even be seen to turn toward the epidermis, but all traces of them are lost as soon as they enter the corium.

The other method of Mallory gives like results as far as the distribution of the nerves beneath the corium is concerned. In cross sections of the tail it is often possible to trace a fibre from the roots leaving the cord out to the corium. Sometimes this may be seen in one section; in many cases two or three neighboring serial sections will show the same. The plexus beneath the corium is shown best, as a whole, in frontal sections of the tail. Here it will be seen that the nerves are *very numerous*, and with the method in hand can be traced to their connections with the cord. There can be no question as to the presence of the nerve-bundle layer of the plexus that Herriek and his pupils have shown; but as regards the stratum of ganglion cells, it seems to me that Schuberg's criticism holds good. At any rate neither of Mallory's methods reveals such a structure, and this would at least seem strange in view of the beautiful staining of other nervous elements. In cross sections of the tail, Mallory's fuchsin method shows nerves running in or immediately beneath the inner corium layer. At times several fibres are in view at once, being, however, of different sizes.

Within the corium the distribution of the nerves to the glands is not apparent in sections which pass through the gland, owing to the exceedingly small size of the fibres. But when the periphery of the gland is just denuded, the nervous elements are shown very clearly. In such cases it will be seen that there is a feltwork of many *very fine fibres* closely investing the gland, *ending upon the muscle fibres and around the nuclei of the gland cells*.

The endings upon the muscles are shown both by Cajal's method and Mallory's fuchsin stain, and in some cases are typical (Pl. XXII, Figs. 25 and 26) as described by Huber and Dewitt ('97) and Coghill ('99). That is, they are equipped with terminal expansions or bulbs which lie on the muscles. In many cases fine branching fibres can be clearly seen lying upon the muscle layer. These pass over ultimately into the finest of slender twigs which without terminal expansions always lie on a muscle fibre and end there (Pl. XXII, Fig. 26.)

The fibres in the perinuclear endings are of much the same character as those of the museles. There are many instances which are very clear of basket structure about the nuclei of the large glands (Pl. XXII, Figs. 21, 22. Pl. XXIII, Fig. 30). I have not been able to discover connections between the fibres and the nuclei, though in at least one case (Pl. XXII, Figs. 23, 24) the fibres end in knobs which lie directly on the nucleus. The latter seems usually to be surrounded only by a basket of fine fibres. Bethe ('94) has described three sorts of endings on cells. Of these he finds that in the unicellular glands of the frog's palate one frequently finds under the nucleus a small blue knob which is connected with a fibre. The latter cannot, however, be followed farther.

In the case of the gland cells under consideration, there can be no doubt that the nuclear basket is connected with nerve fibres. That there should be a nerve supply to the gland cells, seems evident from the experiments of Drasch ('89), Eberth ('49) and Loeb ('96) on Amphibian glands, and we have in *Plethodon* histological evidence of such supply. The well-known influence of the nervous system on the secretion of sweat, for example, may be also mentioned in this connection. Herriek and Coghill ('98, p. 51) have suggested the possibility of a connection between the nerves enveloping the glands, and the gland cells, but were not able to demonstrate it.

The objection may be raised that we are dealing here with elastic instead of nerve fibres. This does not seem possible for several reasons. The elastic fibres, as has been said, show very little variation in size, and never, as shown by staining in orcein, reach the excessive fineness of the nerve fibres. The branching of the elastic fibres is much less frequent than that of the nerves, and, in clearest distinction the former, as seen upon the glands, take an almost uniform direction even in branching, straight toward the epidermis, while the nerve fibres cross and recross and branch in all directions, and the finest twigs show varicosities which are never seen on the elastic fibres. The general effect of the brown fibres in an orcein stain is entirely different from that of the red ones in Mallory's stain, and leaves no doubt of the distinction here set forth between the elastic and nervous fibres.

SUMMARY.

1. The skin glands of *Plethodon oregonensis*, as of most Amphibia, are of two kinds: granular and mucous. The two are distinguished by the character and staining reaction of their secretions, and by other histological features, as well as by the sizes of the glands.

2. The bodies of the large glands possess an investing musculature, and in addition the ducts have both dilator and constrictor muscles lying in the epidermis.

3. The granule glands are poison in character.

4. In the elaboration and ejaculation of the secretion the poison glands are destroyed.

5. Renewal takes place by the growth into all the old glands of a new and smaller gland, which is mucous in character. The presence of this smaller sac is not dependent upon the removal of the secretion of the large glands, for whether this occurs or not, the fundement giving the mucous reaction is found in all glands; in those which show no degeneration as well as in those where it is wide-spread.

6. The growth of the new gland is dependent upon the removal of the secretion about it. There is evidence that even in case the glands are hindered in their development, they still secrete mucus. But when not hemmed in by the heavy granular contents of the large glands they grow and take the place and very probably assume the function of the old glands which they replace.

7. Both musculature and epithelium of the granule glands have a direct nerve supply. The gland cells are surrounded by a basket work of fibres, which in some cases have terminal expansions lying on the nuclei. The muscles are supplied by nerves with typical endings of expansions or bulbs, as well as by fine twigs without terminal expansions.

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April 29, 1904.*

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LIST OF ABBREVIATIONS USED IN THE PLATES.

- con.m.*—constrictor muscle fibres.
c.t.b.—connective tissue bundles.
c.t.l.—connective tissue layer of gland walls.
c.t.—connective tissue in epidermis.
c.w.—cell walls.
d.—duct of gland.
dil.m.—dilator muscle fibres.
el.f.—elastic fibres.
ep.—epidermis.
ep.m.c.—cell containing musculature of duct.
fl.c.—funnel cell.
i.c.l.—inner layer of corium.
l.d.—lumen of duct.
l.gl.—lumen of gland.
m.b.—muscle bundles.
m.c.l.—middle layer of the corium.
m.f.—muscle fibres.
m.gl.—mucous gland.
m.n.—muscle nucleus.
n.c.—nerve cord.
n.e.—nerve endings.
n.fl.c.—nucleus of funnel cell.
n.f.—nerve fibre.
nuc.m.c.—nucleus of mucous cell.
nuc.p.c.—nucleus of poison cell.
nuc.ep.m.c.—nucleus of muscle cell in epidermis.
o.c.l.—outer layer of corium.
p.fl.c.—processes of funnel cells.
p.gl.—poison glands.
pig.—pigment.
prol.m.f.—prolongations of muscles into epidermis.
rep.c.—replacement cell (and nucleus).
rep.gl.—replacement glands.
sec.—secretion.

All the figures were drawn with the Abbé camera lucida.

ERRATA

P. 251, l. 31: *For* fuehsin-orange G-anilin blue,
read fuehsin-orangeG- anilin blue.

P. 259, under Zalesky 1866: *For* Bd. J 1, *read* Bd. 1; *for* Saeyler, *read* Seyler.

P. 264, under description of Fig. 16: *For* $\times 1650$, *read* $\times 825$.

P. 266, under description of Figs. 21, etc.: *For* $\times 1850$ *read* $\times 825$.

PLATE XX.

- Fig. 1.—Cross section of entire tail, showing position on dorsum of large poison glands (*p.gl.*) and the mucous glands (*m.gl.*) chiefly on the ventral side. Diagrammatic except in outlines and proportions of parts. Van Giëson. $\times 22$
- Fig. 2.—Mucus gland from ventral side of tail, showing large lumen (*l.gl.*), and dark staining, angular nuclei (*nuc.m.c.*). Lower part of funnel cell (*fl.c.*) shown in epidermis (*ep*) which is not reproduced entire. Benda's iron haematoxylin. $\times 342$
- Fig. 3.—Poison gland (*p.gl.*) of small size partly replaced by ingrowing mucous gland (*m.gl.*). Funnel cell (*fl.c.*) shown in epidermis (*ep.*); nuclei (*nuc.m.c.*) of mucous gland darkly stained as in Fig. 2. Benda's iron haematoxylin. $\times 342$
- Fig. 4.—Outline drawing of cross section of duct of poison gland showing replacement cells of the funnel (*rep.c.*) rolled one within the other, the funnel cell (*fl.c.*) and the lumen of the duct (*l.d.*) Mallory's conn. tissue stain. $\times 875$
- Fig. 5.—Portion of lower part of poison gland showing bundles of connective tissue (*c.t.b.*) passing from the inner layer of the corium (*i.c.l.*) to the connective tissue layer of the wall of the gland (*c.t.l.*) Nuclei (*nuc.p.c.*) and walls (*c.w.*) of gland cells. Secretion not shown in detail. Mallory's conn. tissue stain. $\times 342$
- Fig. 6.—One side of median longitudinal section of duct of poison gland showing muscle fibre (*m.f.*) and its nucleus (*m.n.*) and the prolongation of the fibre (*prol.m.f.*) into the epidermis (*ep.*). Compare with Pl. IV, Fig. 27. Mallory's conn. tissue stain. $\times 280$
- Fig. 7.—Branching muscle fibres (*m.f.*) from lower part of gland. Mallory's conn. tiss. stain. $\times 342$
- Fig. 8.—Longitudinal section of poison gland through the mouth showing two expansions of muscles (*m.f.*) in which the nuclei lie, and portions of muscle fibres. Nucleus of funnel cell (*n.fl.c.*) at duct (*d.*). Secretion of gland not shown. Ferric-chloride haematoxylin. $\times 342$

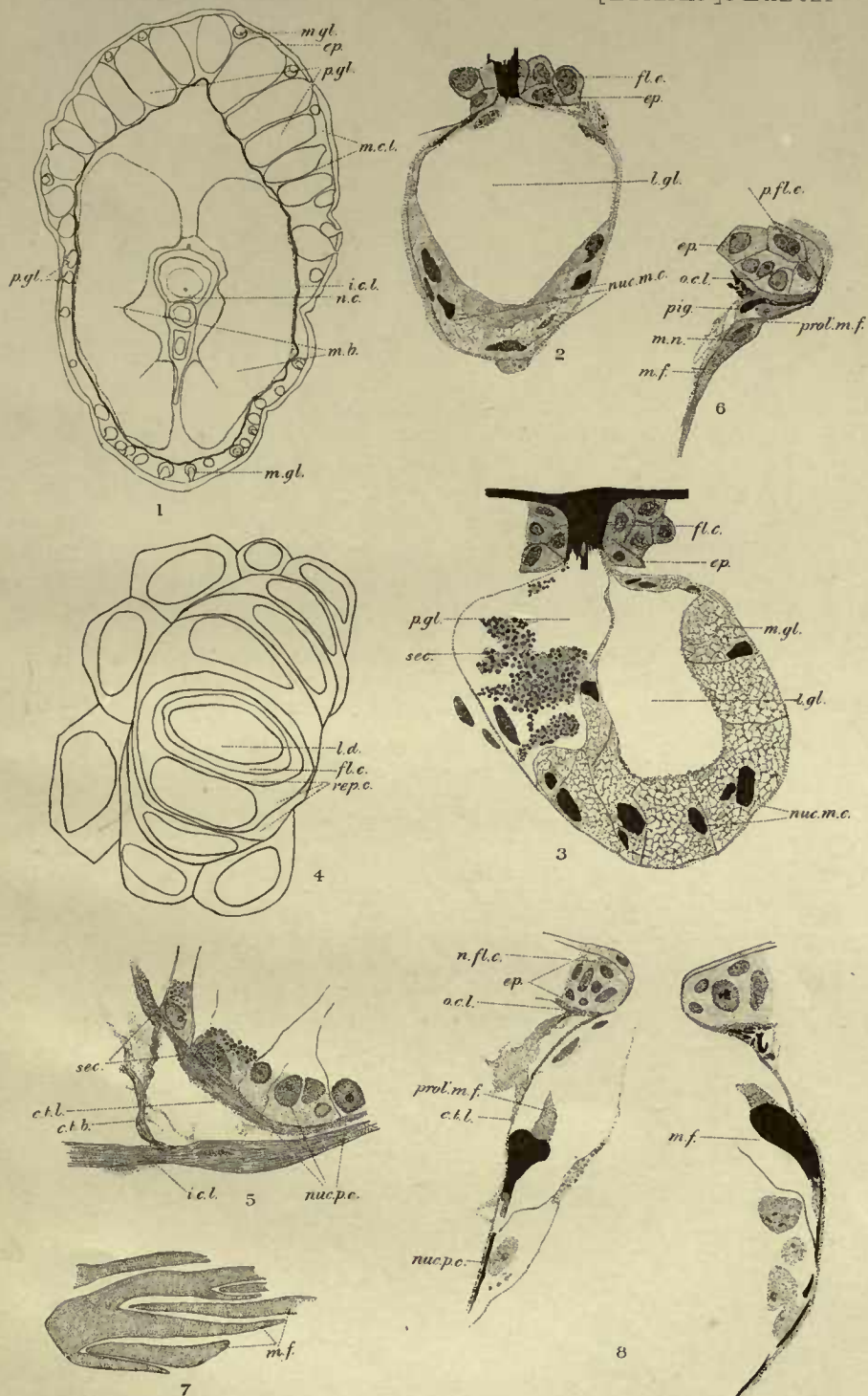




PLATE XXI.

Fig. 9.—Elastic fibres (*el.f.*) on surface of gland. Gland wall (*c.t.l.*) in section indicated; also nuclei of gland cells. The elastic fibres pass through the inner layer of the corium (*i.c.l.*). Tänzer's orcein. $\times 342$

Fig. 10.—Section through upper pole of gland at one side of the duct, showing cut ends of muscle fibres (*m.f.*) and their nuclei (*m.n.*). From cross section of tail. The nuclei in this figure correspond in position to that shown in Pl. XX, Fig. 6, and to the enlargement of the fibres shown in Fig. 8. Mallory's conn. tissue stain. $\times 342$

Fig. 11.—Tangential section through wall of gland and the mouth, from frontal section of tail. Muscle fibres (*m.f.*) and nuclei (*m.n.*) shown. Funnel cell (*f.c.*) lining duct and some secretion (*sec.*) in lumen of duct (*l.d.*). Mallory's conn. tissue stain. $\times 342$.

Fig. 12.—Cross section of gland from frontal section of tail, at level of muscle nuclei (*m.n.*). Compare with Figs. 10 and 11. Van Gieron's stain. $\times 400$

Fig. 13.—Cross section of epidermis at upper pole of poison gland, showing deep lying epidermal cell (*ep.m.c.*) which contains the constrictor and dilator muscles of the duct. Mallory's conn. tissue $\times 342$

Figs. 14 and 15.—Cross sections of ducts at level of cell described in Fig. 13, showing constrictor (*con.m.*) and dilator muscles (*dil.m.*). In Fig. 14, only the outer ends of the constrictor fibre appear. In both figures are shown the ends of the muscle fibres (*m.f.*) of the glands, in the epidermis, and the connective tissue (*c.t.*) outside the muscles. The nucleus of the epidermal muscle cell is shown in Fig. 14. Mallory's conn. tissue stain. $\times 875$

Fig. 16.—Description as for Figs. 14 and 15. But one set of constrictor fibres shown; lumen of duct (*l.d.*) nearly closed. Mallory's conn. tissue stain. $\times 1650$

Fig. 17.—Longitudinal section of nearly empty poison gland. Secretion (*sec.*) very small in amount, cell walls (*c.w.*) distinct, nuclei clear and of irregular shapes. Semi-diagrammatic in unimportant details. Benda's iron haematoxylin. $\times 342$

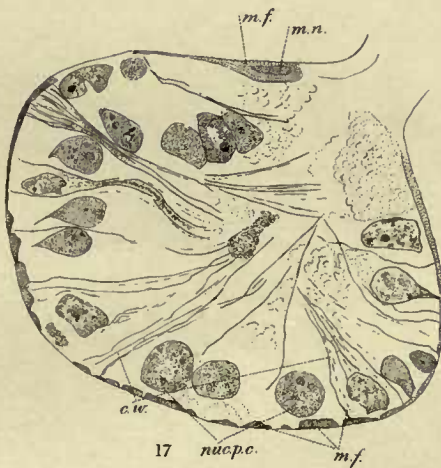
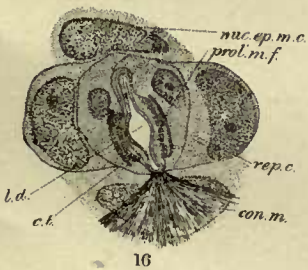
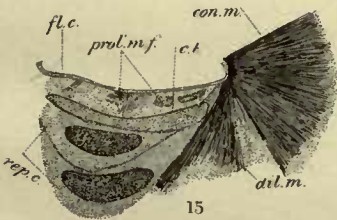
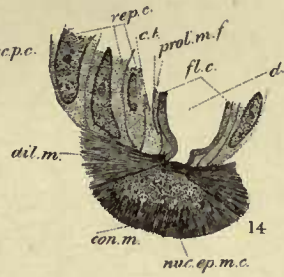
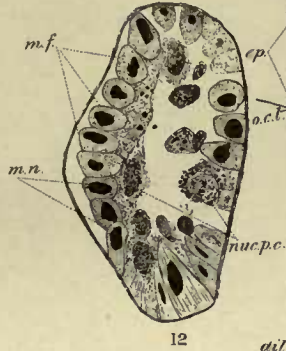
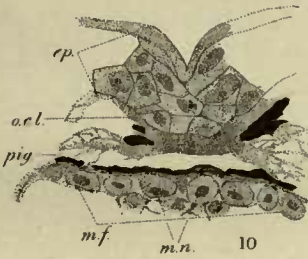
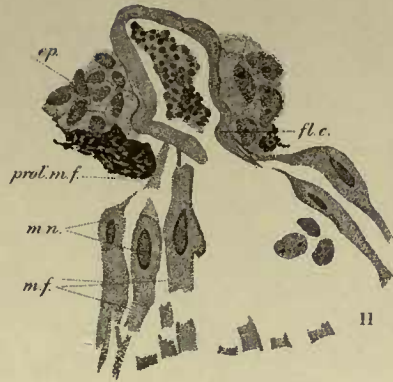
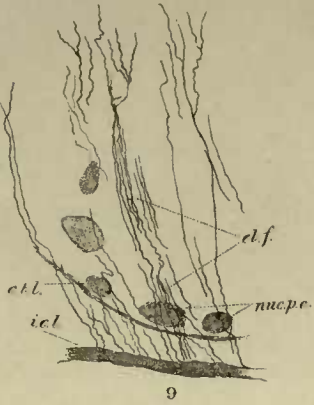




PLATE XXII.

Figs. 18, 19, 20.—Stages in replacement of small poison gland (*p.gl.*) by mucous glands (*m.gl.*) from sides of tail. Mucous nuclei dark. Secretion (*sec.*) shown in poison part only. Benda's iron-haematoxylin. $\times 342$

Figs. 21, 22, 23, 24.—Tangential sections of poison glands, showing nerve endings (*n.e.*) on nuclei of poison cells (*nuc.p.c.*). Mallory's conn. tissue stain. Figs. 21, 22, 24. $\times 1850$. Fig. 23. $\times 875$

Figs. 25 and 26.—Tangential section of wall of poison glands, showing nerve endings (*n.e.*) on muscles (*m.f.*). Fig. 25, Mallory's conn. tissue stain. Fig. 26, Cajal's silver nitrate-pyrogallie acid. $\times 875$

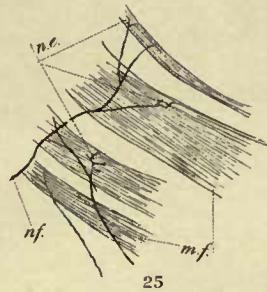
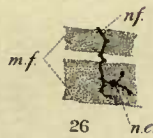
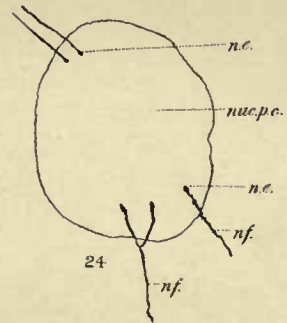
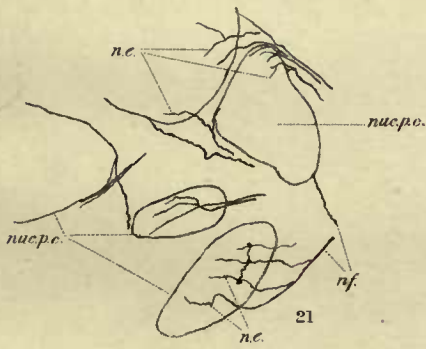
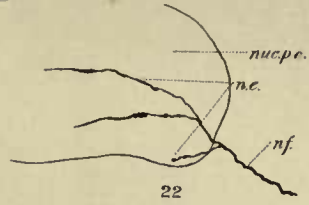
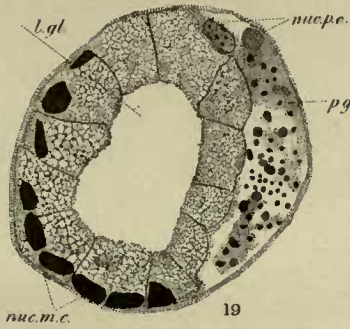
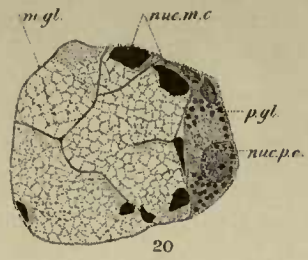




PLATE XXIII.

Fig. 27.—Median longitudinal section of duct of poison gland, showing prolongation of funnel cell (*p.fl.c.*), prolongation of muscles (*prol.m.f.*) into the epidermis, and the connective tissue (*c.t.*) outside them. Replacement cells (*rep.c.*) shown with processes extending down as far as funnel cell. Mallory's conn. tissue stain. $\times 1650$

Figs. 28, 29, 30.—Cross sections of ducts, showing funnel cells (*fl.c.*), gland muscles (*prol.m.f.*), connective tissue (*c.t.*) at sides of duct (*d.*), and constrictor and dilator muscles (*con.m.*, *dil.m.*). Mallory's conn. tissue stain. $\times 1650$

Fig. 31.—Longitudinal section of poison gland, showing small mucus gland (*m.gl.*) inside it. Large gland 440 microns by 180 microns; small gland 90 microns by 43 microns. Mallory's conn. tissue stain. $\times 1650$

Fig. 32.—Nerve-endings (*n.e.*) about nucleus of poison cell (*nuc.p.c.*). Mallory's conn. tissue stain. $\times 1650$



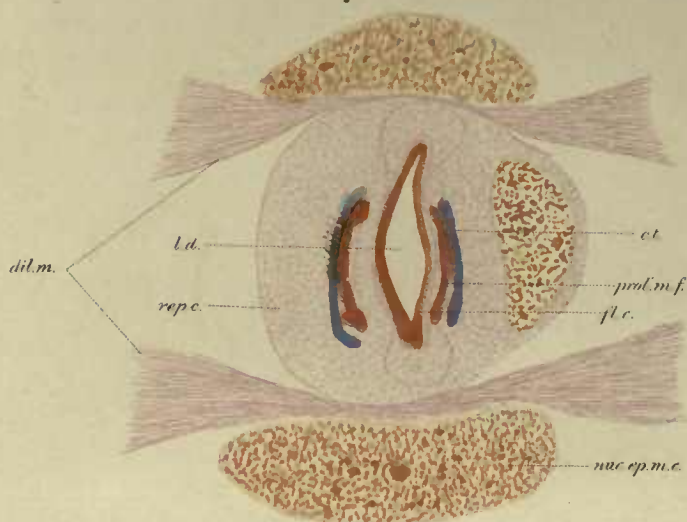


Fig. 23

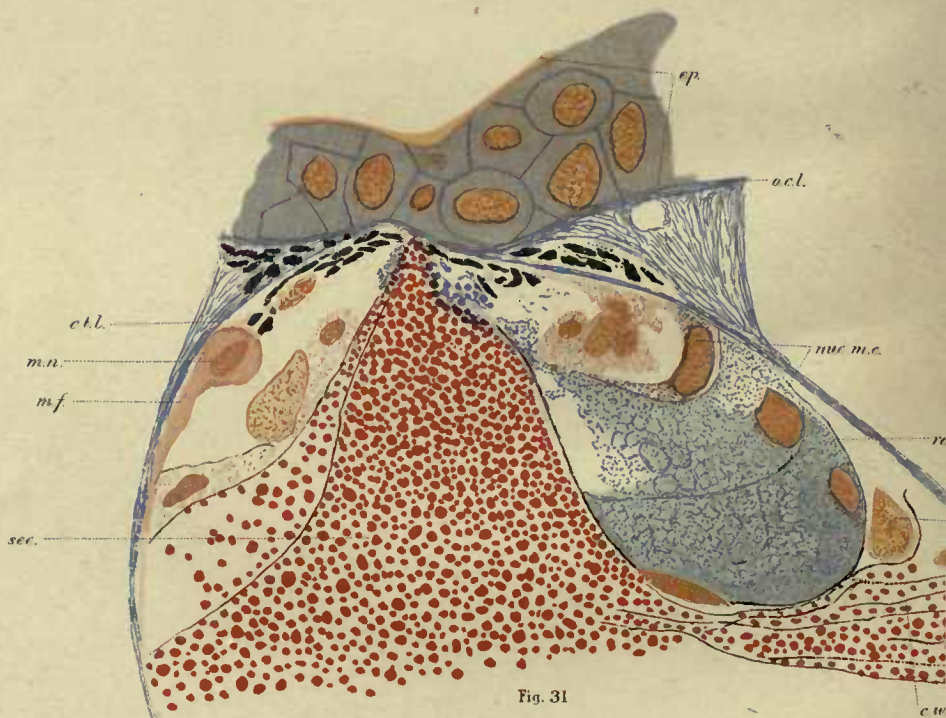


Fig. 31

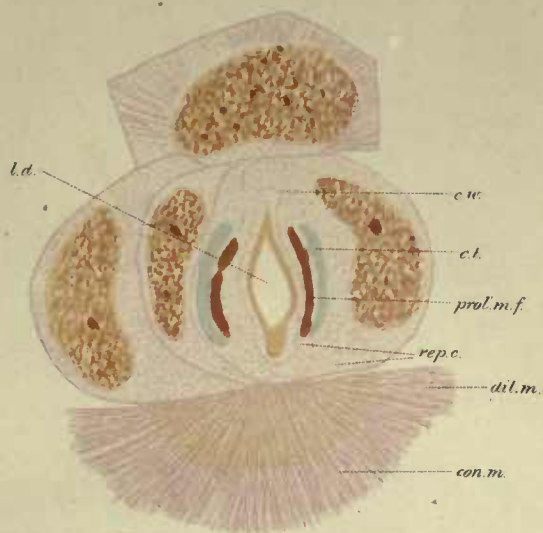
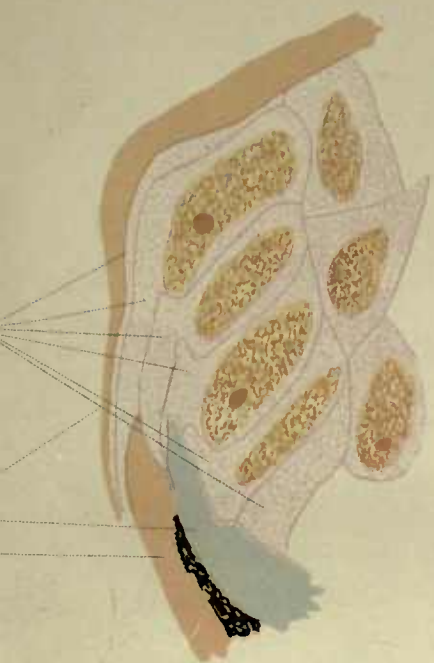


Fig. 29

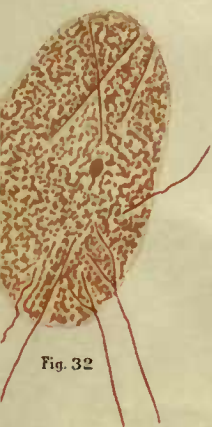


Fig. 32

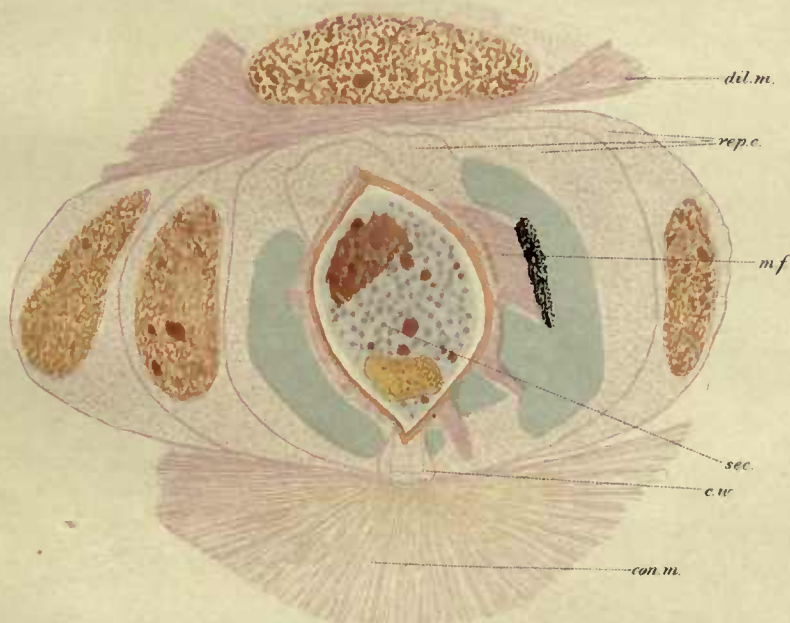


Fig. 30



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